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Surface migration of earthworms in grassland

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With 2 figures

1. Introduction

In 1881, DARWIN reported that healthy earthworms may completely leave their burrows at night and embark on "a voyage of discovery". Over the past century, this migratory behaviour has been little investigated even though it is probable that all earthworm species do emerge from the soil during darkness and crawl about over the ground surface (SCHWERT, 1980; LEE, 1985; MATHER & CHRISTENSEN, 1988).

As earthworms play a significant role in soil structure and fertility (for reviews see: EDWARDS & LOFTY, 1977; SATCHELL, 1983; LEE, 1985), changes in population density can have an influence on the functioning of the soil system. The phenomenon of surface migration may, therefore, have considerable relevance in this respect.

Prior to the present study, casual night-time observations by the authors over several years, encompassing a variety of habitats and weather conditions, revealed innumerable examples of apparently healthy earthworms crawling over the surface of the ground. The following report examines the phenomenon of surface migration in greater detail.

2. Methods

The study site comprised a 4 ha area of permanent grassland on clay soil in Mårslet, east Jutland, Denmark. Within the grassland ran a gravel path, approx. 1 m wide, which proved ideal for investigating the surface forays of earthworms as they travelled from the grassy areas on either side. [Paths were also used by DARWIN (1881) as a means of studying earthworm surface movements].

A few hours after dusk, a length of path (80 m × 1 m) was examined using torchlight by two investigators walking side by side on an outward and return journey, the total duration of the observation period being approximately 20 min per night. All earthworms encountered were collected for further analysis and thereby removed from the study area.

To see whether surface migration was of common occurrence during periods when earthworms are generally active, counts were taken on 10 nights in October/November 1989 (first sampling set) and 18 nights in February/March 1990 (second sampling set). Air temperature (1 m above ground) at the time of sampling ranged from 6.3 to 14.2 °C for the first sampling set, and from −0.9 to 8.8 °C for the second sampling set. For each of these two sets, a different 80 m length of path was examined, the two stretches of path being 200 m apart from each other.

3. Results

In all, 857 individuals and 10 species were collected; all appeared healthy and subsequent examination gave no indications of parasites or pathogens. For the first sampling set (figure 1), a total of 355 individuals was found representing 7 species, number per 20-min

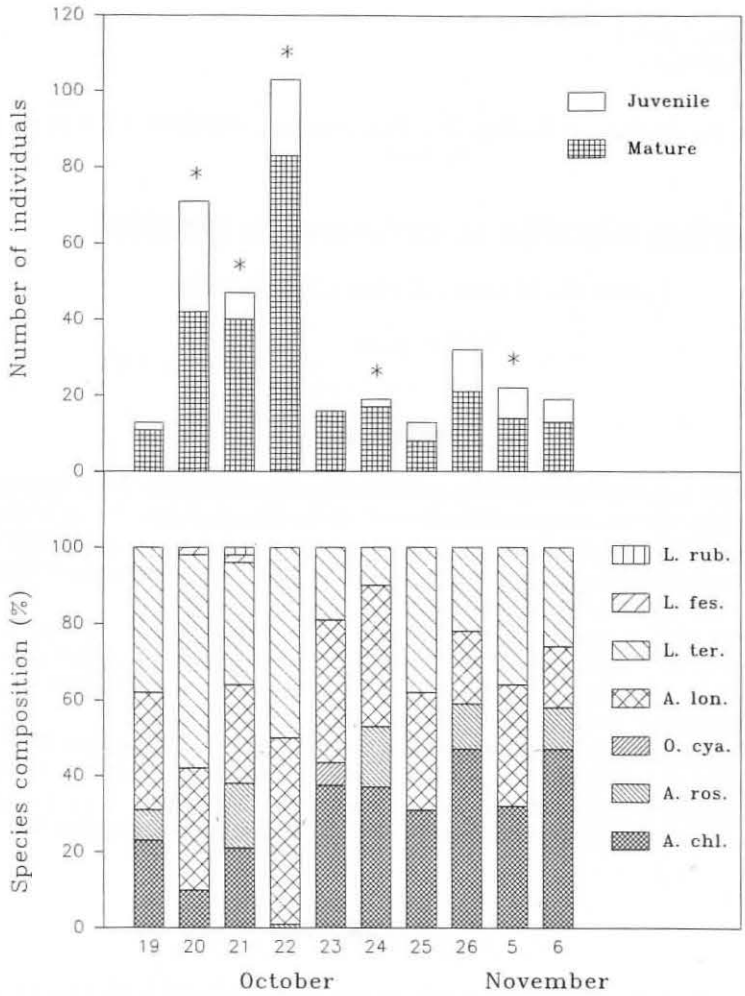

Figure 1. Number of individuals, life stage and species composition per sample for the October/November 1989 sampling set. A length of path (80 m × 1 m) was examined for approx. 20 min per night, commencing between 20.00 h (19.00 h GMT) and 22.00 h (21.00 h GMT). No data were collected over the period 27 October to 4 November. The category 'mature' includes both sub-adults and adults. Extended species names are given in Table 1.
* denotes rain during previous 24 hours.

sample varying from 13 to 103. For the second sampling set (figure 2), a total of 502 individuals was found representing 8 species, number per 20-min sample varying from 0 to 102. For each sampling set, inter-sample variation was also evident for species composition and life stage (see figures 1 & 2).

Climatic conditions such as temperature and rainfall were considered as possible factors underlying the variation in surface migration. All null samples (on 3 occasions) were associated with temperatures below freezing. However, no correlations were apparent for the air temperature range 0 to 14.2 °C occurring over the sampling dates. Rain during the previous 24 hours tended to increase total number of earthworms migrating (MANN-WHITNEY $U = 17.5$, $p < 0.001$, $n = 25$), this trend holding for both mature ($U = 18.0$, $p < 0.001$, $n = 25$) and juvenile ($U = 32.0$, $p < 0.01$, $n = 25$) individuals. Even so, surface migration was evident during dry weather.

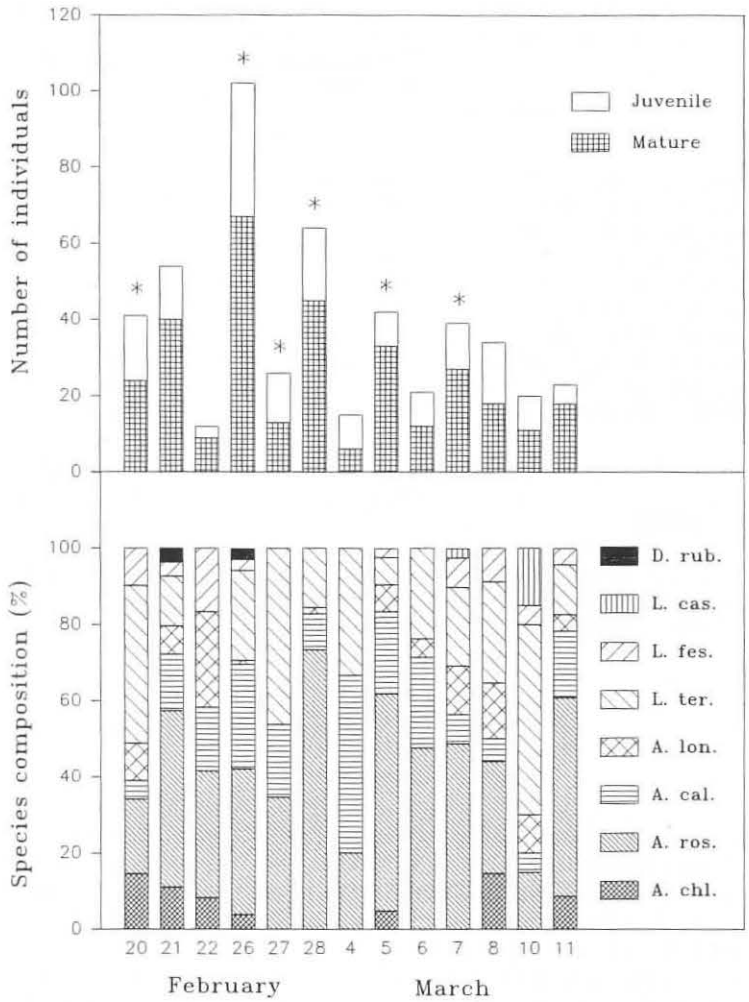

Figure 2. Number of individuals, life stage and species composition per sample for the February/March 1990 sampling set. Another length of path (again 80 m × 1 m) was examined for approx. 20 min per night, commencing at 22.00 h (21.00 h GMT). No earthworms were evident on 1, 2 and 9 March when temperatures fell below zero. No data are shown for 23 February and 3 March due to totals of 5 or less individuals. No data were collected over 24/25 February. The category 'mature' includes both sub-adults and adults. Extended species names are given in Table 1.
* denotes rain during previous 24 hours.

The cumulative totals for each sampling set are presented in table 1. The predominant species in the first sampling set were *Lumbricus terrestris* (LINNAEUS, 1758), *Aporrectodea longa* (UDE, 1885) and *Allolobophora chlorotica* (SAVIGNY, 1826), whereas those in the second sampling set were *Apporectodea rosea* (SAVIGNY, 1826), *L. terrestris* and *Aporrectodea caliginosa* (SAVIGNY, 1826). Concerning the change in species composition from the first to the second sampling set, the main trends apparent were a decrease in *A. longa* (−28.2%), *L. terrestris* (−17.1%) and *A. chlorotica* (−13.9%), but an increase in *A. rosea* (+37.7%) and *A. caliginosa* (+16.9%). With regards to life-stage, mature individuals (i.e. sub-adult and adult) predominated over juveniles by 3:1 and 2:1 for the two sampling sets, respectively.

Table 1. Cumulative totals (%) for species composition and life stage for each sampling set.

	First Sampling Set (n = 355)	Second Sampling Set (n = 502)
Species:		
Dendrodrilus rubidus (SAVIGNY, 1826)	0	1.0
Lumbricus castaneus (SAVIGNY, 1826)	0	0.8
Lumbricus rubellus (HOFFMEISTER, 1843)	0.3	0
Lumbricus festivus (SAVIGNY, 1826)	0.6	4.0
Lumbricus terrestris (LINNAEUS, 1758)	40.0	22.9
Aporrectodea longa (UDE, 1885)	34.4	6.2
Octolasion cyaneum (SAVIGNY, 1826)	0.3	0
Aporrectodea caliginosa (SAVIGNY, 1826)	0	16.9
Aporrectodea rosea (SAVIGNY, 1826)	5.3	43.0
Allolobophora chlorotica (SAVIGNY, 1826)	19.1	5.2
Life stage:		
Juvenile	24.8*	34.7*
Mature (sub-adult & adult)	75.2*	65.3*

Species order depicts the trend in habit from litter-dwelling (first four species) to deep-burrwing/surface foraging (next two species) to soil-dwelling (remainder).
* = significant difference between pair ($p < 0.001$; χ^2 test).

4. Discussion

We here wish to stress that although the phrase "surface activity" occurs frequently in the literature (KOLLMANSPERGER, 1955; SATCHELL, 1967; EDWARDS & LOFTY, 1977; MACDONALD, 1980, 1983), this tends to refer to surface feeding (usually with tail in burrow) by a single species, *L. terrestris*. In contrast, our study deals with the surface forays of fully emerged earthworms, and involves a variety of lumbricid species. Furthermore, we point out that although occasional mass emergence of earthworms has aroused much curiosity over the past century, including several reports by early naturalists (DARWIN, 1881; PRYTZ, 1916; FRIEND, 1921, 1924), most occurrences of mass emergence coincide with adverse events such as water-logging due to heavy rainfall (LANKESTER, 1921; MERKER, 1926, 1928; NISHIDA, 1950; DOEKSEN, 1967), flooding by rivers (ADIS & BOGEN, 1982; ADIS & RIGHI, 1989), onset of dry/cold seasons (GATES, 1961, 1972; REDDY, 1980), and arrival of predators (MADGE, 1969). The present study, however, is not restricted to such environmental adversities.

Our direct observations of fully emerged earthworms in the present study, as well as those over several years, indicate that surface migration is commonplace and can involve many individuals and several species. This finding is supported by data from pitfall traps in pasture land in France where a total of 1104 individuals and 8 species was found when sampled twice monthly over a 13 month period (BOUCHÉ, 1976). For both investigations, although sub-surface migration and subsequent emergence due to encounter with the obstructing gravel path or pitfall trap is a possibility, surfacing for this reason alone seems improbable. Our study permitted the observation of earthworm behaviour prior to sampling, and many instances of emergence from the soil followed by surface migration in various directions were apparent within the adjacent open grassland.

We regard the surface migratory behaviour of earthworms reported here to be a normal activity in the field, as is also indicated by the numerous and often long surface trails which

are easily recognisable in a variety of habitats, such as agricultural fields, parkland, gardens etc. (DARWIN, 1881; MATHER & CHRISTENSEN, 1988).

In several respects, our findings on surface migration appear to be at variance with traditional views on earthworm behaviour prevailing in the literature. For example, earthworms are generally considered to be a relatively sedentary group of organisms, and yet in our study – despite the short duration of the sampling period per night – often considerable numbers of earthworms were found migrating (up to 103 in 20 mins), implying relatively high mobility. This mobility within the population is further stressed by a recent temporal investigation involving the monitoring (at 2-h intervals) of earthworms crawling over the path during the night, which indicates that surface migration continues throughout the hours of darkness (J.G.M. & O.C., unpublished). Another example concerns the idea that earthworm species normally inhabiting the soil are less mobile than those dwelling in surface-litter (SATCHELL & STONE, 1977); however, the high abundance of emerged, migrating specimens of soil-dwelling species such as *A. rosea*, *A. chlorotica* and *A. caliginosa* in our study (the cumulative total for these 3 species alone for the entire study being 45%) seems contrary to this. Also, although *A. caliginosa* is sometimes considered not to be an active surface migrant (EIJSACKERS, 1983), it becomes evident from our investigations that this species does indeed in fact migrate over the soil surface.

During the course of our longer-term observations, we have seen partly and fully emerged individuals of several species feeding on the soil surface, ingesting soil or grazing algae on stones. These species include not only the deep-burrowing/surface feeding *L. terrestris* and *A. longa* but also the so-called soil-dwelling *A. rosea*, *A. chlorotica* and *A. caliginosa*. This suggests that acquisition of food is one reason for surface migration.

The migratory ability of earthworms is further highlighted by measurements of their surface trails; single forays may involve distances greater than 13 m (DARWIN, 1881) and 19 m (MATHER & CHRISTENSEN, 1988) from the point of emergence from the soil. Such migratory potential may seem surprising compared with estimates of colonisation rates for earthworm populations, namely from less than 1 m to up to 10 m per year. However, it should be noted that these estimates are based on the introduction of earthworms to sites under reclamation, such as polders (VAN RHEE, 1969; HOOGERKAMP, ROGAAR & EIJSACKERS, 1983), pasture devoid of earthworms (STOCKDILL, 1982), refuse tips (BROCKMAN, KOEHLER & SCHRIEFER, 1980), and pulverised fuel ash (SATCHELL & STONE, 1977). Consequently, we regard such low estimates merely to measure a population's gradual establishment within a sub-optimal habitat.

Although not the main aim of this report, consideration of climatic variables suggests some influence on surface migration. Generally speaking, more earthworms are likely to migrate with increased humidity due to rainfall. A similar positive influence of precipitation has been found for the surface feeding activity of *L. terrestris* [KOLLMANSPERGER, 1955; SATCHELL, 1967; MACDONALD, 1980, 1983]. Nevertheless, our longer-term observations confirm that migration occurs over a wide range of climatic conditions, including dry periods and even thaw after snow. Emergence of earthworms during the spring thaw has also been reported in America (GATES, 1961).

The pronounced seasonal variation in species migrating in the present study, i.e. the marked increase in the proportion of soil-dwelling species such as *A. rosea* and the concomitant decrease in the deep-burrowing/surface feeding species such as *A. longa* and *L. terrestris* towards Spring, is probably a reflection of species-specific differences in phenology (seasonal differences in number and/or general activity) (see reviews by EDWARDS & LOFTY, 1977, and LEE, 1985).

The marked predominance of mature earthworms surface migrating in our study may well result from one or several factors combined. For example, current population structure (i.e. proportion of juvenile:mature individuals) may underly the observed trend. Also, the cost of migration in terms of predation risk may play a part; most observed instances of attack on emerged individuals by carnivorous carabid beetle larvae involved smaller, juvenile earthworms. In addition, sexual activity resulting in a higher incidence of migration by

mature earthworms may likewise contribute; we have noted instances of fully emerged adults of several species mating on the soil surface, as well as emerged individuals of various species attempting to enter the burrow systems of other individuals.

5. Conclusions

On the basis of numerous observations, we propose that surface migration by earthworms is primarily a routine resource-seeking activity aimed at locating food and mates. This routine behaviour is likely to be enhanced by favourable environmental conditions such as high humidity. Furthermore, we propose that surface migration aimed at locating shelter or a more suitable habitat can be precipitated by natural and anthropogenic disturbances such as attack by predators, flooding of the soil, and also agricultural practice. Mass migration of earthworms is simply an extreme response to extreme conditions. Thus, migration incidence is likely to reflect ambient conditions, i.e. increased migration due to a lowering of habitat suitability, and *vice versa* (see also BAKER, 1978; AIDLEY, 1981; MATHER & CHRISTENSEN, 1988).

Therefore, we wish to challenge certain generalisations regarding earthworm behaviour. We conclude that surface migration is a far more common phenomenon than previously supposed, and that many species – litter-dwellers and soil-dwellers – are in fact active surface migrants.

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Earthworm surface migration was examined by recording the number of individuals crossing a gravel path in an area of grassland during periods of the year when earthworms are generally active. In all, 857 individuals and 10 species were observed migrating (20-min observation period × 28 nights). Surface migration was carried out by juvenile and mature earthworms, but predominantly the latter. Both litter-dwelling and soil-dwelling species were active surface migrants. This study provides the first quantitative data derived from direct observations of surface migratory activity for several species of lumbricid earthworms. It is proposed that surface migration is primarily a routine resource-seeking activity aimed at finding food and mates, though migration aimed at seeking shelter or locating a more suitable habitat can be precipitated by natural and anthropogenic disturbance. It is concluded that surface migration – a hitherto poorly documented activity – is an important component of the behavioural repertoire of many earthworm species.

Key words: Lumbricid earthworms, surface migration, colonisation, habitat suitability, resource-seeking behaviour, natural and anthropogenic disturbances.

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